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THE ROMANCE OF DOMESTICATED PLANTS[1]

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Man's fate is closely correlated with events of the distant past—events which occurred even before he existed. One such incident occurred about 225 million years ago, which was new among plants and eventually greatly changed the vegetative landscape. This accident resulted in the formation of a plant organ which we recognize as a seed. Heritable changes were not common in these more primitive seed-plants, but finally during the Cretaceous period (about 120 million years ago), the Angiosperms made their appearance. All of our common seed-bearing plants belong to this group, excepting the conifers. This new kind of propagule was unique in that it contained an embryo plant which resulted from a sexual union. Free water was not necessary in the fertilization process. Food accumulated in the embryo and in surrounding tissues of the seed, which could be used in further growth of the embryo and in germination. This new plant organ could withstand desiccation yet remain viable for months to hundreds of years. In many instances, it could survive low temperatures which ordinarily would kill vegetative parts of the same plant. The nature of this organ was such that it could, at maturity, become widely deciminated within its habitat and to other habitats by several natural agencies.

By means of this new kind of propagule a very successful land flora became established even over relatively arid regions, on all the continents except the antarctic. All land habitats were more fully occupied by plants than before. The total vegetation mass was greatly increased, which in turn changed the characteristics of soils. The stream of heritable variations which occurred in seed plants is almost beyond comprehension. These mainly occurred before there were any humans in existence. The beginnings of some understanding of such matters is but a century old. Taxonomists now recognize about 10,000 genera and at least 200,000 species of seed plants. Many more will undoubtedly be discovered as time goes on.

SOME HERITABLE VARIATIONS IN SEEDS

Perhaps it is trite to point out that probably in every species of seed plant certain heritable potentialities may become expressed only in the seeds. Such were some of the characters in garden peas (*Pisum sativm*) L. which Mendel studied in his classical work of nearly a century ago—smooth and wrinkled seed coats, and yellow and green. From these seed characters (fig. 1)[3] as well as variable

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characters from other parts of the pea plant, the fundamental principles of heredity applicable to both plants and animals, were discovered. Though lost for nearly forty years, these principles when rediscovered, sparked the new science of genetics with the beginning of the twentieth century. However, peas were not new to man in Mendel's time. They are among his oldest domesticated plants, the oldest recognizable remains dating 3000 B.C. from the Swiss lake dwellings of the Stone Age. The place of origin is in doubt, but may have been in the Mediterranean region or in Western Asia. The pea as we know it is a cultigen and botanists have been unable to locate it in the wild state.

The kidney bean (figs. 3, 4) (*Phaseolus vulgaris*), probably originated in Brazil. However, its greatest diversity was reached in Guatamala and Mexico. The Peruvians were cultivating it about 4,500 years ago. It was widespread among North American Indians. More that 500 varieties have been given names in recent times. Much the same story may be told for the Lima Bean (*Phaseolus lunatus*) (fig. 2). This illustration shows something of the remarkable diversity of Lima Beans as to size, shapes and color patterns. These are from a collection of present-day varieties found in Guatamala and Mexico. These two species of beans are sources of basic food materials used by millions of people.

The Carob, Locust-bean, or St. John's Bread (*Ceratonia siliqua*) a leguminous tree of the Mediterranean region (fig. 5) has pods which are used for human consumption as well as feed for swine and cattle. The pods have been identified by some with the locusts of John the Baptist. The term "carat" has been applied to the Carob-bean or seed, and these seeds were used originally as a unit of weight, the Carat. When mature, the seeds seem to be fairly uniform in size, are very hard and the seed-coat is impervious to water until it is scarified. This matter of the seed-coat being impervious to water is a heritable characteristic and is found in the seed-coats of many species. It is of concern to horticulturists, agronomists, foresters and botanists. The water-proof coats of seeds and some fruits is obviously correlated with longevity of the embryo. The most prominent example is that of East Indian Lotus (*Nelumbo nucifera* Gaertn.) (fig. 7) These are botanically fruits with a single seed inside. The fruit coat (pericarp) is the structure which is impermeable to water. When the fruit coat is notched germination may occur within ten days. A quantity of these fruits were recently discovered in the depths of a peat bog in southern Manchuria. The seeds were viable and would germinate readily upon scarification of the pericarps. By the Radiocarbon technique these seeds were shown by Libby in 1951 to be about 1,000 years old. The seeds and rhizomes have been used as food by peoples of Asia for many centuries. The North American species, the water chinquapin (*Nelumbo lutea* Willd.) Pers., was used as a source of food by the Indians.

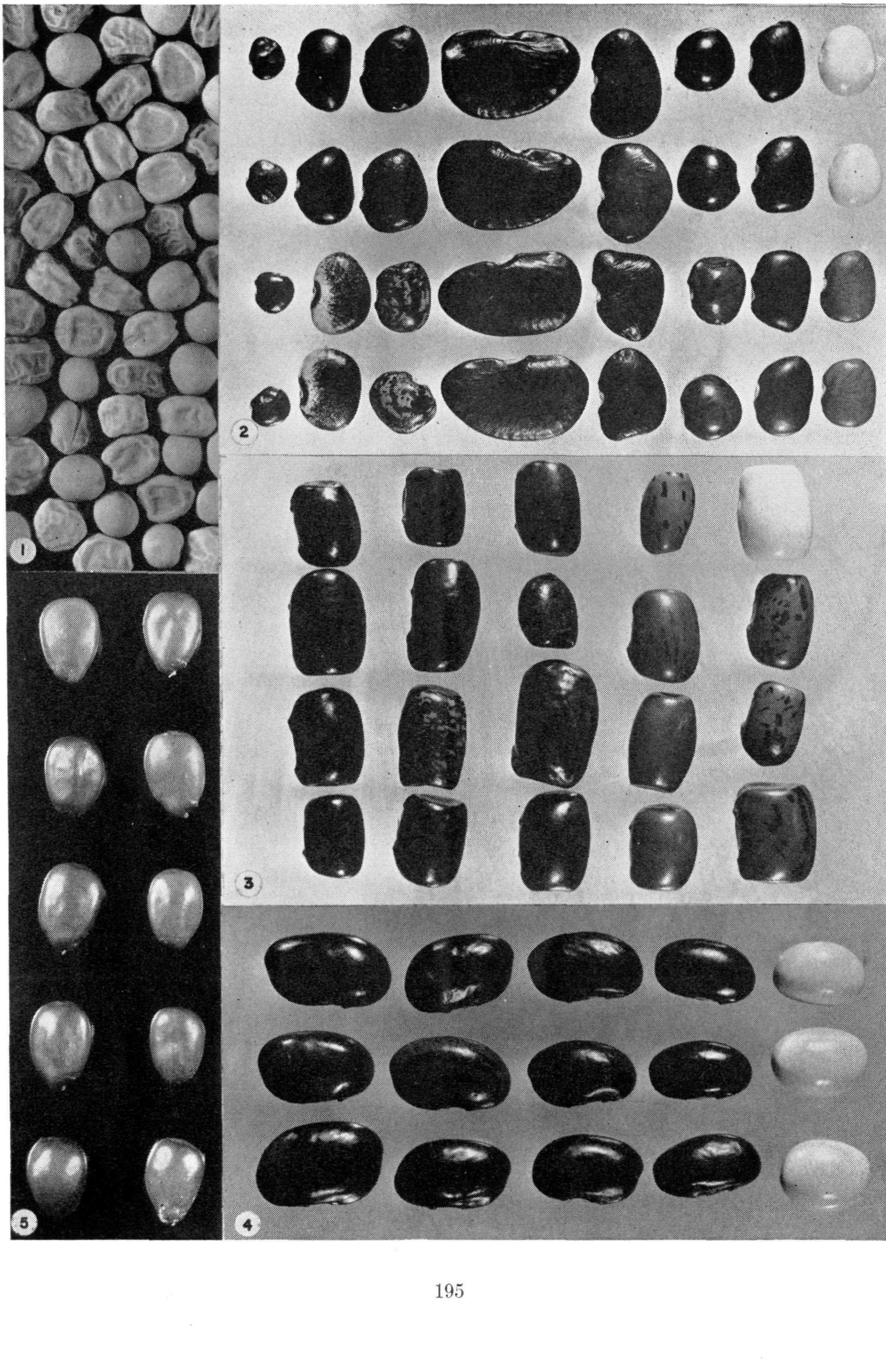
In any seed collection one of the most conspicuous to be found is the Castor-Bean (*Ricinus communis*) (fig. 6). This is not a legume but belongs to the spurge family. Though widely naturalized through the tropics, it probably originated in Africa with India as a second best choice. In the seed coats we find remarkable variations in colors and patterns, as well as size and shapes of the seeds. In addition, the endosperm synthesizes castor-oil which youngsters would readily proclaim as being different from any other, as a vile substance which should never have happened. In addition to its medicinal value, it is of importance industrially.

EXPLANATION OF FIGURES IN PLATE I

1. Garden Pea (*Pisum sativum*) seeds.
2. A collection of Lima Bean (*Phaseolus lunatus*) seeds from Guatemala, varying in size, shape, color and seed-coat patterns. Most of the dark colored areas are shades of red.

3–4. Common bean (*Phaseolus vulgaris*) seeds from Guatemala and Mexico. These and the Lima Beans of figure 2 are from a collection made by Mr. Webster McBride.

5. Seeds of St. John's Bread (*Ceratonia siliqua*).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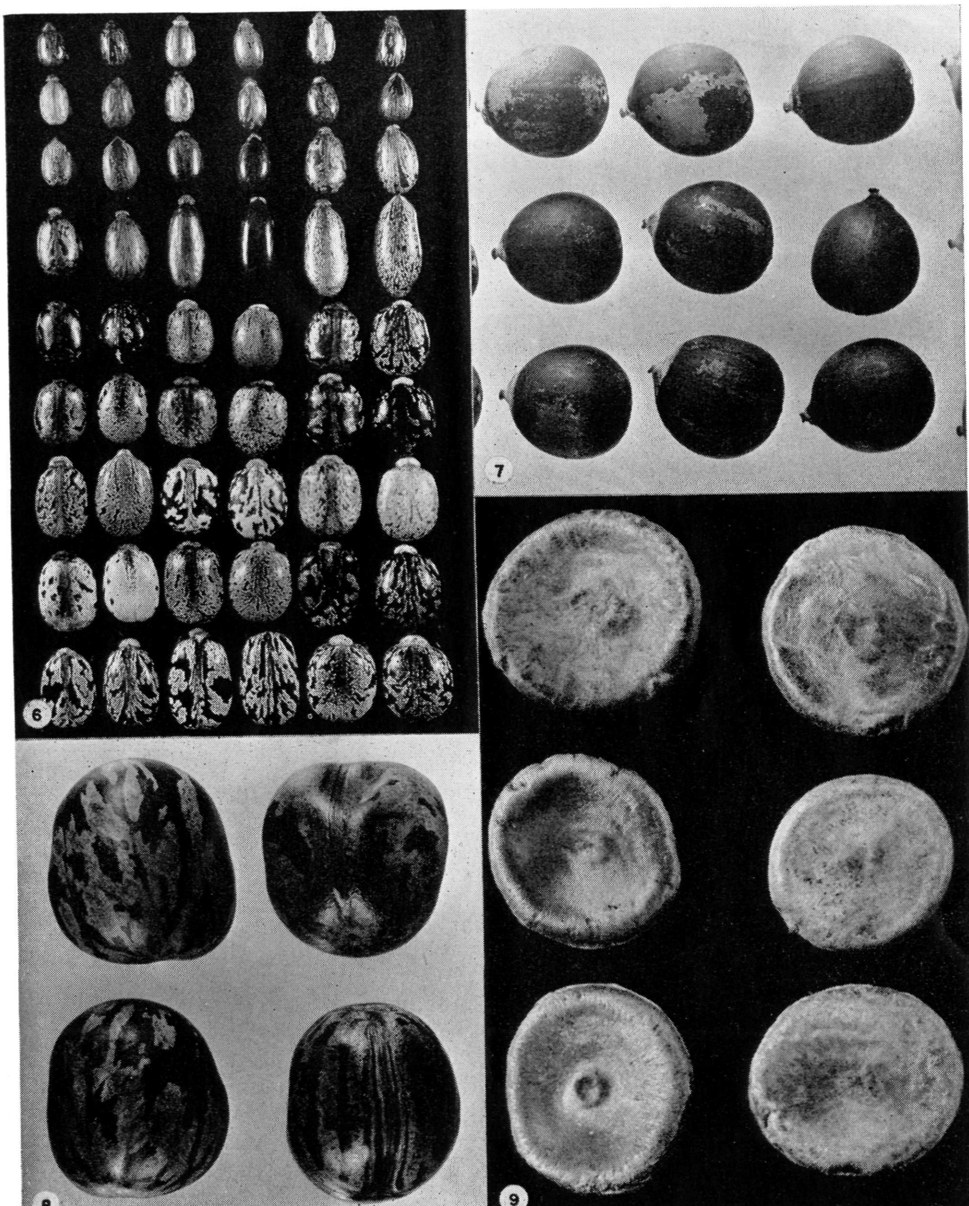
Another member of the spurge family is the Para Rubber tree (*Hevea brazilensis*) with a few of its unusual seeds (fig. 8) exhibiting characteristic patterns. It is a native of the Amazon. Although found in negligible amounts in the seeds, a latex with high rubber content is synthesized in the vegetative parts of the plant. This tree is the chief source of natural, commercial rubber. Although the natives are said to have learned to make rubber balls from the latex, a crude syringe, and was used for water-proofing some clothing, nothing was done about domestication until recent decades. I need not dwell upon the importance of rubber in modern economy, but only need to mention our experiences after the Pearl Harbor disaster.

Highly pigmented seeds are found distributed rather widely among plant families. The Sword Bean (*Canavalia gladiata*) (fig. 11) from tropics of the Old World. The large seeds are edible and they are used as ornaments. The Rosary Pea (*Abrus precatorius*) (fig. 10), another bean from tropics of Asia has a hard, scarlet coat with a black spot. They are used extensively in the tropics for beads, rosaries and other ornaments. The powdered seeds made into a paste and applied to arrows or darts make any wound fatal in about 24 hours. Seeds of the Strychnine Tree (*Strychnos nux-vomica* L.) (fig. 9), native of India and Indo-China, are disc-shaped and about an inch in diameter. These seeds yield the very poisonous substance known as Strychnine, and is of importance medicinally. Another species of *Strychnos*, native of South America yields curare, a deadly poison used by natives for poisoning arrows, and is now coming into importance in modern medicine.

The dye known as Annatto from the "Lipstick Plant", (*Bixa orellana*) (fig. 12) used in the coloring of oleomargarine is a tropical American Species. The dye is made in the outer soft, red layer seen in the illustration. This layer is an extra seed coat which is found in some species and is known as an aril. The spice known as Mace is from the aril of the nutmeg seed. When you eat the Chinese fruit called the Litchi, you eat only the fleshy aril. Another seed with an aril (fig. 13) is from the Bird-of-Paradise flower, (*Strelitzia nikolai*), a mat of tangled orange-colored hairs which grow at one end of the seed. And another (fig. 14) the seed of the Traveler's Tree (*Ravenala madagascariensis*) with the membranous, metallic-blue colored aril enfolding the seed. This metallic-blue pigment is unusual among plants. These two last species belong to the banana family. In either case the arils are of no use to the plants. Yet, these continue to develop on each new crop of seeds and from generation to generation.

Seeds may vary through out-growths from the seed-coat, forming wings, spines and hairs. Cotton seeds (fig. 17) is an extreme example with long hairs growing from the entire surface of the seed coat. These hairs of the cotton certainly have no survival value to the plant, in fact they are a disadvantage to distribution of the seeds in the wild state. There are many varieties of cotton (*Gossypium*) derived from indigenous species from both the Old and the New World. It is known that some Peruvians were cultivating cotton and were weaving textiles from it in 2500 B.C. Most of the cotton in cultivation in the United States is of American origin. These varieties have 52 chromosomes while the African and Asiatic varieties have 26 chromosomes and will not hybridize except on rare occasions. Because of this the Old and New World types have remained distinct even though they were brought together in our southern states in the earlier periods of cotton culture. Although the species of the two types will not readily cross, the hairs or fibers from the seed coats are very similar. It is remarkable that widely separated primitive peoples of the two hemispheres, independently learned to make textiles from the cotton fibers and domesticated the plants more or less simultaneously.

Variability in dimensions and weight of seeds may add to our appreciation of this plant organ. In various acid soil areas in Ohio, a native orchid, known as the Rattlesnake Plantain (*Goodyera pubesens* (Willd,) R. Br. may be found.



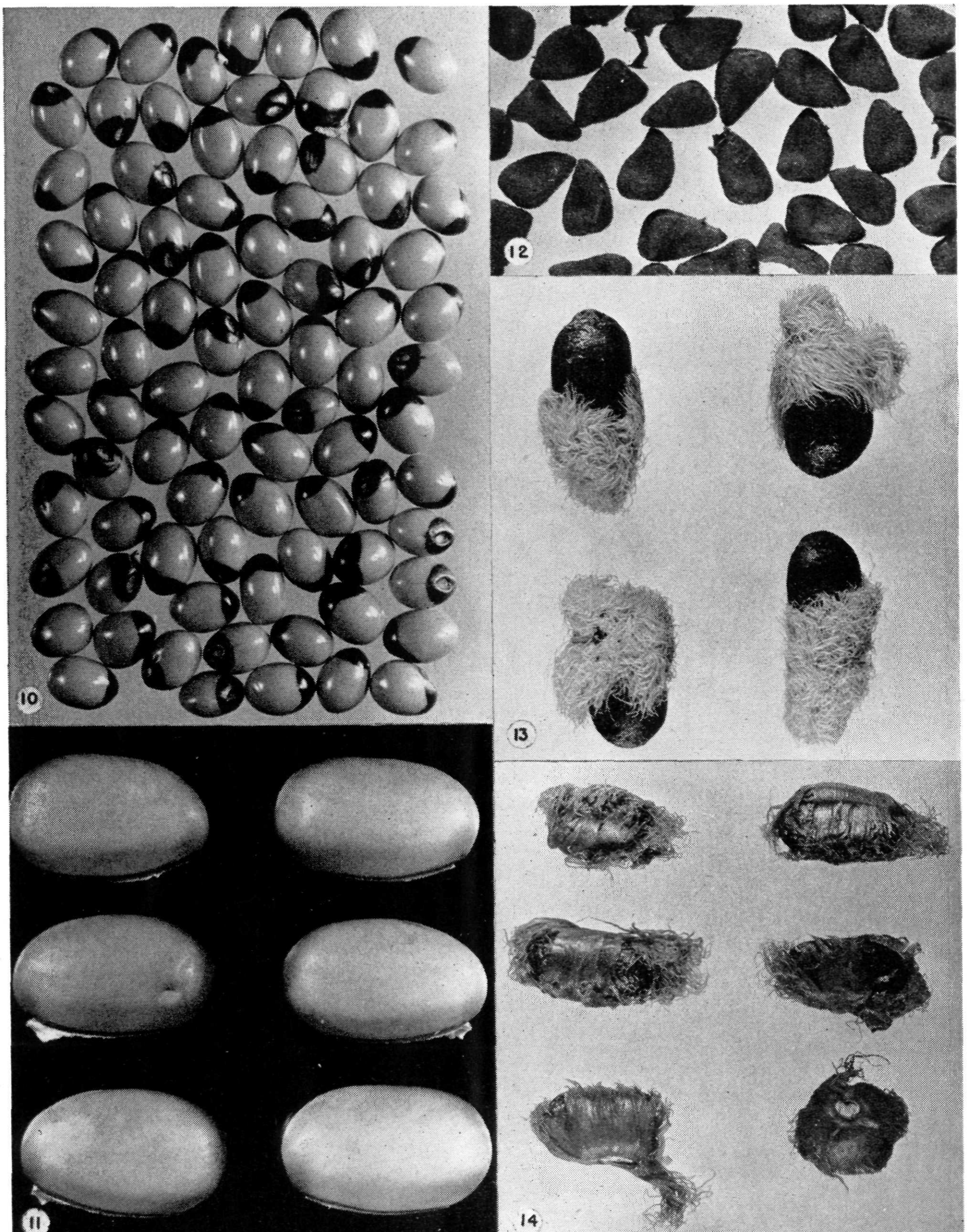
6. Castor-bean seeds.
7. Fruits of Lotus (*Nelumbo lutea*).
8. Seeds of Para Rubber Tree (*Hevea braziliensis*).
9. Seeds of Strychnine Tree (*Strychnos nux-vomica*).

The seeds (fig. 16) of this plant are among the smallest known. The dimensions of this magnified specimen is approximately 0.02 in. long by 0.003 in. wide (641.4X 95.3 microns). The weight is about .000002 g., or in other words, it takes 2 million of these seeds to weigh a gram. Many other orchids have seeds with dimensions and weight in about this category. In addition, one of the tropical orchids is known to bear about a million seeds to a flower or fruit.

The natives of the Seychelles islands in the Indian Ocean and Oriental lands bordering this body of water, are accustomed to find a somewhat monstrous object (fig. 15) washed upon the beaches. For centuries it was thought to be a product of the ocean and was called *coco de mer*, with many legends and superstitions developing about it. The hollowed-out shell was highly valued by potentates of the Orient as containers for drinking water. The shell was believed to contain an antidote to any poison which might have been added to the water. In the early part of the 19th century the fan palm (*Lodoicea sechallarium*) was discovered growing on Praslin island. The nut or stone and seed are ordinarily two-lobed, appearing as though two large coconuts had partially joined, and are now commonly called the Double Coconut. Occasionally a three-lobed stone is found, which has led to the fallacy that a single fruit may bear from two to three seeds. There is but one seed to a fruit, which is usually two-lobed, about 13 in. wide and 12 in. long with a weight of about 40 lb.—the largest seed known!

If we were asked to pick out the plant family which is of greatest importance to man and other mammals it undoubtedly would be the grasses (Graminaceae). There are over 5,000 species of grasses known, having a world wide distribution, from aquatic to desert habitats and from the tropics to the arctic. The grains of grasses are botanically fruits—a fruit with a single seed, which adheres to the membraneous fruit coat or pericarp. This illustration (fig. 18) is a microscopic, longitudinal section of a corn grain. The fruit coat is evident as a thin tissue surrounding the relatively large seed. The embryo is in the lower part of the grain, with the remaining large mass of tissue, the endosperm. This tissue is unique in that it develops ordinarily from the fusion of three nuclei, a male gamete and two nuclei of the embryo sac which are identical genetically to the egg or female gamete. Since these three nuclei are each haploid, the endosperm nucleus, which results form the three nuclei fusing, is triploid, or has the $3n$ number of chromosomes or 30 ordinarily in corn. Since all the cells of the endosperm tissue are decedents of the triple fusion nucleus, all the cells of the endosperm are triploid. While this is occuring, another male gamete fuses with the egg. The fertilized egg or zygote then is diploid or has the $2n$ number of chromosomes, which in corn ordinarily is 20. By cell division the zygote becomes an embryo, every cell of which is diploid, and as the growth including cell division continues, maturity of the plant is attained, with all the cells of the roots stem and leaves being descendents of the fertilized egg, each having the diploid number of chromosomes.

The corn endosperm (fig. 18 E) is noted for the great accumulation of foods, carbohydrates and protein. It is a basic food source for many people and it has no equal as feed for farm animals. Last year (1952) 3,306,000,000 bushels grew on the farms of the United States. Numerous genetic variations (fig. 21) occur in the endosperm, as to kind of carbohydrate, the physical qualities and pigmentation. In this illustration six fundamental endosperm types are shown on the ear—Floury, Dent Starchy, Flint, Sweet, Waxy and Pop. The Floury type of endosperm has a high percentage of starch in relation to the protein content, is soft and readily ground by the primitive methods of the Indians and was a common variety with them. Our common field corn varieties are of the Dent Starchy type. The Flint type of endosperm is hard and horn-like, and was cultivated extensively by the Indians. Sweet corn although known by the ancient Peruvians and by a few of the North American Indians in the latter part of the 18th century, it never became important with them, and white man became interested in it about a century



10. Rosary Pea (*Abrus precatorius*), scarlet with a black spot about the hilum.
11. Sword Bean (*Canavalia gladiata*) seeds of a purplish-red color and an inch or more in length.
12. Seeds of Annatto (*Bixa orellana*) with velvet-like coat of a maroon color. These with the *Abrus* of figure 10, were supplied by Capt. Wm. A. Fuller, Cocoa, Fla.
13. Seeds of Bird-of-Paradise Flower (*Strelitzia nikolai*) with a brilliant orange-colored aril.
14. Seeds of the Traveler's Tree (*Ravenala madagascariensis*), with the membranous, fringed, metallic blue aril enfolding them.

ago. Waxy corn is characterized by the presence of a waxy carbohydrate, erythrodextrin. Its culture history is uncertain. The Indians apparently made no use of it. Geneticists in this century found in it a useful tool in certain genetic studies and preserved stocks for that purpose. When World War II came along, cutting off the supply of Cassava—used in the manufacture of tapioca—a considerable acreage of hybrid waxy corn developed, with the erythrodextrin used in the making of tapioca and postage stamp glue. Popcorn seeds have a hard, horny endosperm which explodes when heated, forming the white, soft, spongy mass of this popular confection. It was known and used by the ancients of Mexico and Central America.

This illustration (fig. 22) shows the results of crossing a pure line red flint plant with a pure white flint corn plant. The ears borne on the white plant as a result of the cross pollination will be red grained and the embryo in every grain will be hybrid. When these hybrid grains are planted, and the mature, hybrid plants are self pollinated, the resulting ears will show a segregation of three red grains to one white, a typical, simple Mendelian ratio. If a pure white grained plant is pollinated with pollen from a hybrid individual, the ear developing on the white plant will show a 1:1 ratio of red to white grains,—and demonstrate the "back-cross" of the geneticists. Because of these heritable variations and many others, corn or maize has become one of the most important tools in the study of heredity.

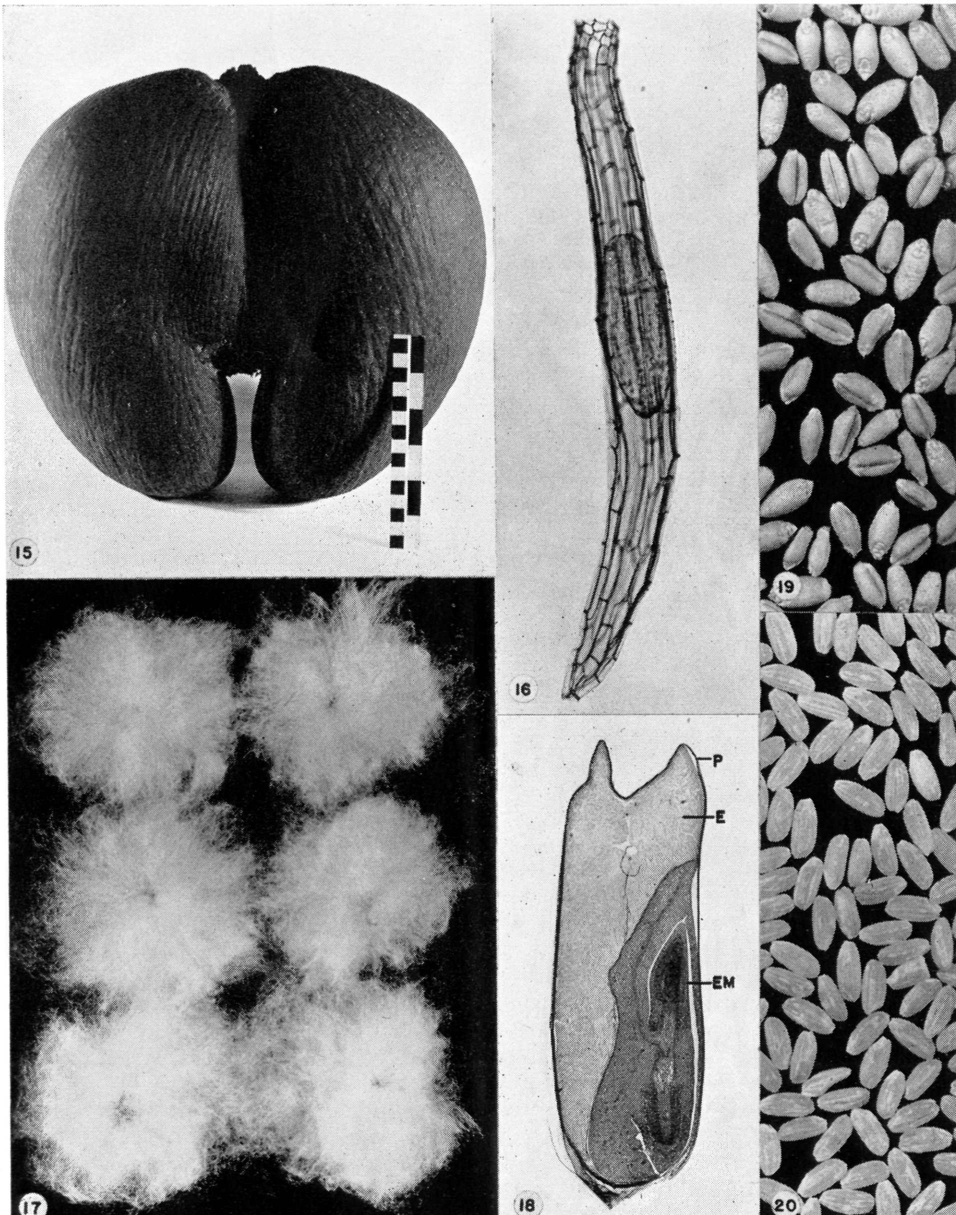
Wheat (*Triticum aestivum*) (fig. 19) is another grain of the grass family, which has been in cultivation for a least 5,500 years. The earliest remains were found in Mesopotamia. The grain is not as large as the maize grain, but has a large endosperm with starch and protein having accumulated in it. The wheat seed is a basic source of food, serving nearly half the human population of the world. In the United States the wheat yield was 1,291,000,000 bushels in 1952.

Some place in southeastern Asia, rice (*Oryza sativa*) (fig. 20) became domesticated earlier than 2,800 B.C. Over 5,000 varieties have been recorded. The wild ancestor is unknown. The rice seed is a basic source of food for nearly a billion people.

MAN AND HIS DEPENDENCE UPON SEED PLANTS

By the beginning of the great Ice Age, the Pleistocene Period, 1,500,000 years ago, the world stage of vegetation became set in such a way that our modern seed plants (angiosperms) were highly developed. A new actor began to make appearances on this stage—he was known as man. He was able to survive because of the right kind of food supply from the abundant flora, materials were available from which he could make clothing, construct shelter, use as fuel for warmth and solace for his ailments. He was a wanderer, endowed with intelligence far superior to any other animal, and had inherited knowledge of how to survive passed on to him by his primate ancestors. It was essential for him to have intimate knowledge of the plants which were useful to him as well as those which were harmful—developing the rudiments of plant taxonomy. He learned to make weapons in protecting himself from other animals, and eventually to use these animals for food and their skins for clothing. Some groups learned to live almost entirely by hunting, making it necessary to follow the herds. Some remained as gatherers of food, or perhaps some combination of the two methods of livelihood. They learned to care for particular trees perhaps which bore desirable fruit. In the digging for edible roots, bulbs, tubers, and rhizomes, they became aware of vegetative propagation.

Some of the more botanically minded noticed that some of the seeds they ate had sprouts on them, and upon looking further saw various seedling stages through to mature plants bearing the same kind of seed. The discovery of these relatively simple processes and attendent relationships were no doubt slow and torturous—even as we find it today for some college students in general botany! Primitive



15. Double Coconut, the largest seed known.
16. A photomicrograph of Rattlesnake Plantain seed, among the smallest known. The oval body is an embryo within the seed-coat.
17. Cotton seeds.
18. Longitudinal section of a corn grain with the membranous pericarp (*P*), large endosperm (*E*) and the embryo (*Em*).
19. Wheat grains.
20. Rice grains.

man learned not only to collect and plant the seeds but to care for them in various ways. He learned how to store them for the interval between collecting and planting, how and where the planting should be done. He observed that when planted in some organic waste, that the plant grew better and bore more seeds and fruit. He became aware of differences in the various popagules and selected for planting those which appeared most desirable to him. These were the beginnings of horticulture and agriculture.

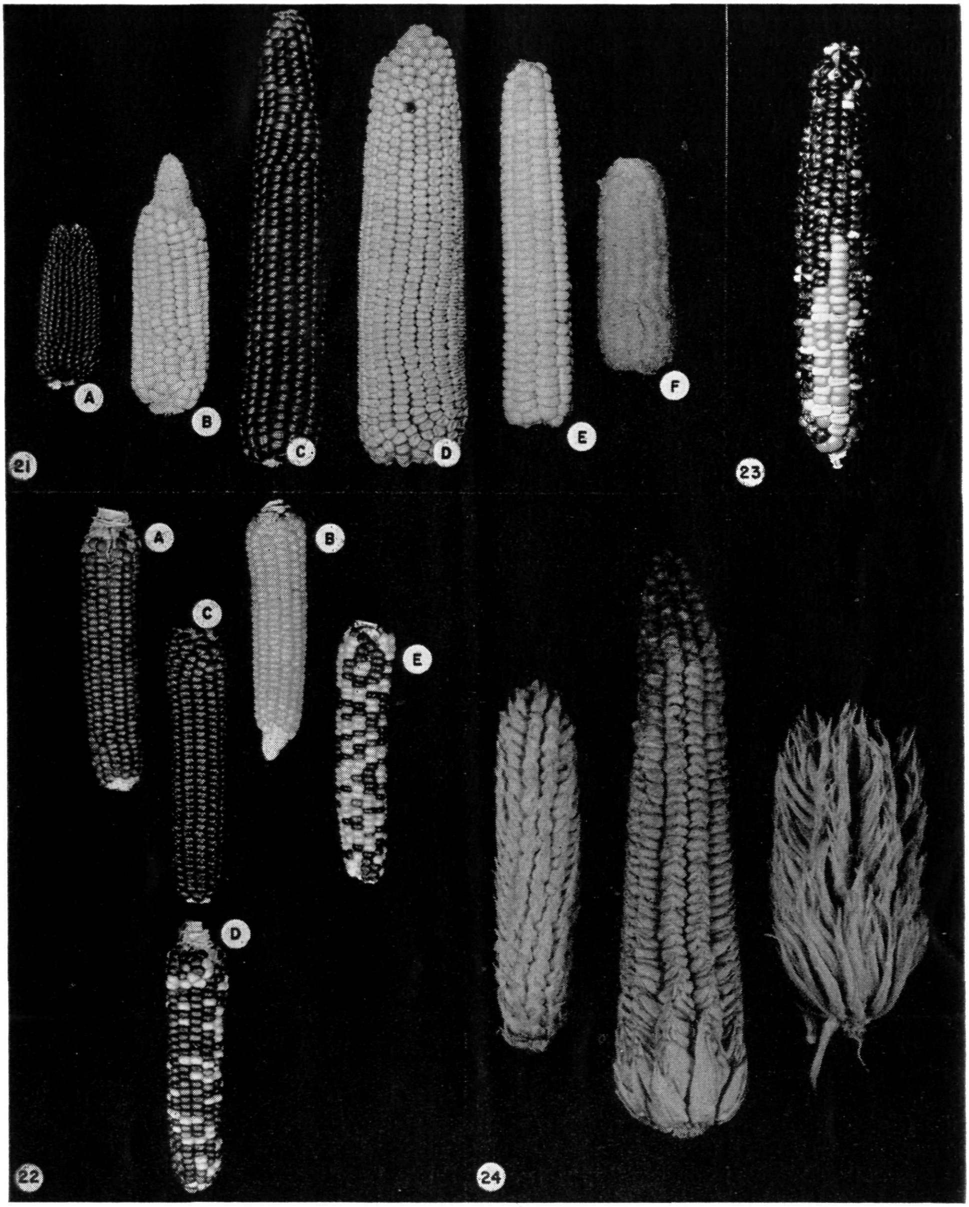
As the primitive hunters populated the continent of their origin, some groups migrated to other continents when opportunities arose. A land bridge once existed from Africa across Sicily to Italy, over which plants and animals, including early man probably migrated. Due to the vast accumulation of water in the form of glacial ice, sea levels were lowered to the extent that land connections were possible between Siberia and North America, in the area of Bering Strait. The bands of Asiatic hunters entered Alaska by this route, eventually populating both North and South America. The most direct route would cover more than 5,000 miles from Arctic through tropical climates, establishing a great number of primitive cultures, eventually leading to the establishment of the classic civilizations of the Incas, Myans, and Aztecs, within a period of about 15,000 years. Though fantastic, this is based on the best inferences of archeologists and geologists.

The movement of the Siberian primitives into North America must have been slow, perhaps taking many human generations. They came from a cold northern region which probably had no agricultural plants. There is no evidence for even a single species of domesticated seed-plant having arrived from Europe, Africa or Asia in pre-Columbian times. It is possible that man arrived in North America before there were any domesticated plants in Asia or elsewhere, and that domestication of plants in this hemisphere may have occurred more or less simultaneously with that in the Old World. As these people moved into the Americas they came in contact with a vast, new seed-plant flora with geneplasms very different from those experienced by their ancestors. The Indians are known to have made use of over a thousand species of native plants in what is now the United States. Out of these only the sunflower and Jerusalem Artichoke can be regarded as domesticated. However, many species were added to the list from Mexico, Central America and South America.

DOMESTICATED PLANTS NATIVE TO THE AMERICAS

A partial list of the more important plants domesticated in pre-Columbian times may help us visualize and appreciate the efforts of the first people of the New World. Maize or Corn with perhaps more than 8,000 varieties should head the list and is the only important cereal which originated in the Americas; The Potato in its many varieties, now a staple food source used by many millions of people; No vegetable counter is complete without Sweet Potatoes the year round, also a great source of commercial starch; Cassava, a staple food in the tropics, and a source of waxy carbohydrate used in the manufacture of Tapioca; fine pastries are made from the starch of Arrowroot and Canna; Lima beans in considerable variety; Kidney beans from which snap beans, soup beans, and field beans developed; millions of tons of Tomatoes are annually consumed in the United States today; Hot and Sweet Peppers widely used as condiments and to camouflage left-over ground meats; Tobacco, introduced into Europe about 450 years ago has become the "sovereign master of practically all mankind"; another narcotic—Coca, the plant which yields cocaine, with 15,000,000 South Americans as addicts; Coca or Chocolate; Annatto—a vegetable dye, now used extensively for the coloring of oleomargarine, butter and cheese; Peanut Squash, Pumpkin and the Chayote; and important fruits such as the Pineapple, Avocado, Papaya, Guava, Custard Apple and the Sapodilla.

It may be pertinent to point out here that all the *basic* food plants, upon which



21. Six endosperm types of corn, *A* Red Pop, *B* Waxy, *C* Red Flint, *D* Yellow Dent Starchy, *E* White Flour, *F* Sweet Corn.
22. Pure Red Flint (*A*) corn, White Flint (*B*), Hybrid (*C*), Ear from selfed hybrid (*D*) showing segregation; and (*E*) with a 1 : 1 ratio of red to white grains, resulting from a back-cross of a hybrid (*C*) with the recessive white (*B*).
23. An ear of Variegated Maize with a block of white and yellow grains near the base, which are the result of a mutation having occurred.
24. Pod corn ear variation.

we are dependent, came into existence in pre-Columbian times. No new, basic food plant has developed from the wild species, in either hemisphere, since that time. The Concord, Catawaba and Delaware grapes derived from our native fox grape, the Cranberry derived from the wild species, long used by the Indians; the Modern Strawberry has resulted from hybridization of the North American species and a Chilean species. The above grapes, cranberry and strawberry developed during the 19th century, and in the present century the blueberry has been added. Important as they are, these can scarcely be regarded as basic food plants.

HOW DOMESTICATED PLANTS DIFFER FROM WILD SPECIES

Domesticated plants differ from wild species in that the domesticated species ordinarily cannot survive without human assistance. This service is characterized by planting (sowing or propagating), protecting, selecting and preserving. Most of the activities in horticulture and agriculture are concerned with how these practices may best be accomplished.

Heritable variation is the rule among seed plants rather than the exception. The frequency of these variations may be high for some species and low in others. The quality of the variation may range from something that is of great value in survival of the species growing in the wild, to characters which are neutral, through degrees of inhibiting influence to lethal variations. It should be kept in mind that such variations occur in an individual plant of a species, and never simultaneously in all individuals in the population of a given species. If one wishes to observe such variations, he must study individuals for these variations. The early horticulturalist had incentive to observe and tend individuals rather than large segments of a population in his small garden, since he was dependent on the small patch for food. Any variation discovered which met his needs better, were selected, protected, preserved and finally propagated. The variation was selected because it suited his purposes better and without regard to the survival value of the plant growing in the wild state. If good enough, from his standpoint, he would plant his whole plot to the variant and eliminate the less desirable ancestral type. Other members of his tribe planted it too, and eventually many groups in a large area were culturing the new and desirable variant. Additional variations occurred from time to time and were allowed to accumulate. Eventually the accumulated heritable differences were so great that the wild ancestor was no longer recognized, and the domesticated form was attributed to a Diety of this or that. This is true for a large number of domesticated plant species from both the eastern and western hemispheres. It was mentioned earlier for the garden pea. It appeared to be true for wheat, (until recently), rice, potato, tobacco and others, with maize or corn as the crowning example.

The wild ancestor of corn is unknown. It has either become extinct, or is so different in appearance that it has not yet been recognized. There is some evidence that pod corn was cultivated by the Cochise Indians of Arizona about 3,000 years ago (fig. 24), Pod corn differs from ordinary maize in that each grain on the ear is enclosed in a husk (bracts of the spikelet bearing the grain). The pod character is controlled by a single dominant gene. Some have regarded this as being the original wild corn. This notion has been questioned, since pod corn is no more able to survive in nature without the aid of man, than is ordinary corn. The pod-character is readily transmitted to any other variety of corn by cross pollination, resulting in a new combination or a recombination of characters. A similar case was mentioned earlier in which white flint corn was crossed with red flint. Any of the many varieties of corn will readily cross. This hybridization went on in gardens of primitive man and undoubtedly occurred more rapidly than in the wild state, because of the greater concentration of plants.

In some plants, with maize as the outstanding example, the hybrid (heterozygous) individuals are more vigorous than either of the parents. Man was unaware of this hybrid vigor (heterosis) until Shull discovered it in 1908 and 1909. This discovery was not put into practice for almost 25 years. Now, about 90 percent of corn acreage is hybrid. As a result of using hybrid seed for planting as much as 25 percent increase in yield may result. This ranks as one of the greatest achievements in plant breeding.

Some place in the area from Mexico to Honduras, in pre-Columbian period, there is some evidence that maize crossed with *Tripsacum* (Gama-grass) and from the hybrid or its segregates Teosinte (*Euchlaena*) resulted. The crossing of these two genera is difficult, but it has been accomplished in a few instances by Mangelsdorf and Reeves, through a special technique. The chances for it to occur in nature are remote. However, Teosinte has a set of chromosomes which appear like those of corn and a set similar to *Tripsacum*. Taxonomists have given Teosinte the rank of a new genus (*Euchlaena*) since it is so different from either *Tripsacum* or Corn. If the above story is true, we have the unusual case of hybridization between two genera resulting in a third genus of grasses. The early Indians did not make much use of teosinte as a domesticated plant, but is used now to some extent as a forage plant.

FIGURE 25. The common Day-Lily (*Hemerocallis fulva*, clone *Europea*).

A CAUSE OF STERILITY IN SOME HYBRIDS

Hybridization between two rather distantly related individuals often results in the hybrid individuals being sterile. This sterility may be due to differences in the chromosomes from the male parent and the female. These differences may not prevent fertilization taking place when the male gamete comes in contact with the egg-cell. If this occurs in Day-Lily (*Hemerocallis fulva*) the sperm would have 11 chromosomes and the egg would have 11 chromosomes. The fertilized egg or zygote would have 22 chromosomes or the diploid number. There is no orderly arrangement of the 22 chromosomes within the zygote nucleus. The zygote divides mitotically resulting in two new cells which are identical, as far as the chromosomes are concerned, and each would be identical to the zygote from which they came. In the same way, since the leaves, stems and roots become initiated from the embryo by the same kind of cell divisions, it becomes evident that all cells of the vegetative plant are identical. This continues to be true for the flower parts up to and including the so-called mother-cells of the anthers and ovules. The mother cells are the immediate forerunners of the gametes. However, it is common knowledge that gametes (sperms and eggs) have the monoploid number of chromosomes or half the number found in any cell of a leaf stem or root. The reduction from the diploid number to the monoploid occurs in the first two divisions of the mother cells in the anthers and ovules. The sperm of a Day-Lily, as stated above, has 11 chromosomes which we might label *a*, *b*, *c*, *d*, *e*. *f*, *g*, *h*, *i*, *j*, and *k*. An egg cell of this same kind of plant has 11 chromosomes which are similar and could legitimately be labeled from *a* to *k* when the egg and sperm fused, there is a random assortment of these two sets of chromosomes in the zygote, and this is continued throughout all vegetative or somatic cells, to and including the mother cells of- the anthers and ovules. However, at this point, the chromosomes become assembled in pairs within the mother cell nucleus, *a*, pairing with *a*, *b* with *b*, and so on through the *k*-pair. As division continues, the members of each pair of chromosomes separate, moving to opposite poles, with a wall eventually separating the two groups. The two new cells have half the number of chromosomes found in the mother cell. If this is occuring in the anthers, the end result will be male gametes; if in the ovule, the egg cells will develop. The diploid phase starts again upon fusion of a sperm and egg.

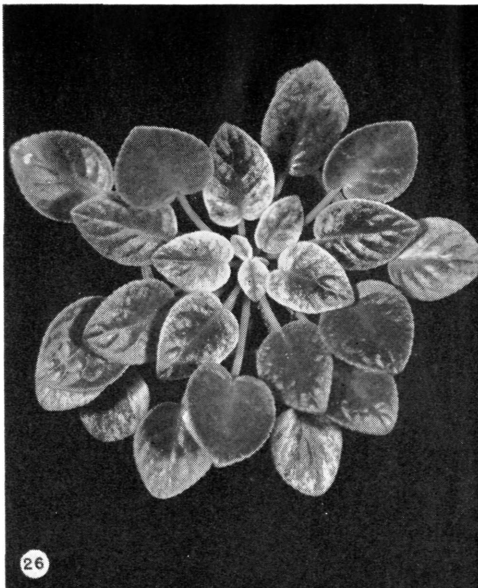
However, if one of the sets of 11 chromosomes, let us assume, form the egg, were sufficiently different that we would have to label them *p*, *q*, *r*, *s*, *t*, *u*, *v*, *w*, *x*, *y*, *z*, pairing of the chromosomes previous to the reduction divisions usually will not take place, and the cells abort. Ordinarily no fruit or seeds can develop. This is what apparently happens in the common Day-Lily (*Hemerocallis fulva*, clone *Europea*), (fig. 25). This Day-Lily was introduced from Europe perhaps over a century ago. Although no fruits or seeds ever develop, it propagates readily from the rhizomes. It is found thoroughly established along roadsides and railroads in every county in Ohio—dumped there as waste from someone's garden.

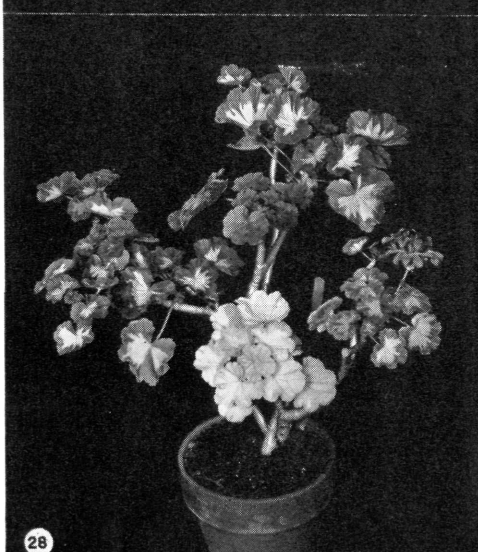
The seedless fruit varieties of orange, grapefruit, pineapple, banana, grapes and persimmons are further examples of sterility because of irregularities in gamete formation, but differ from the Day-Lily in that the pistil of the flower, although sterile, does not abscise, but continues to grow and matures as a seedless fruit. Such plants cannot survive in the wild, without the aid of man.

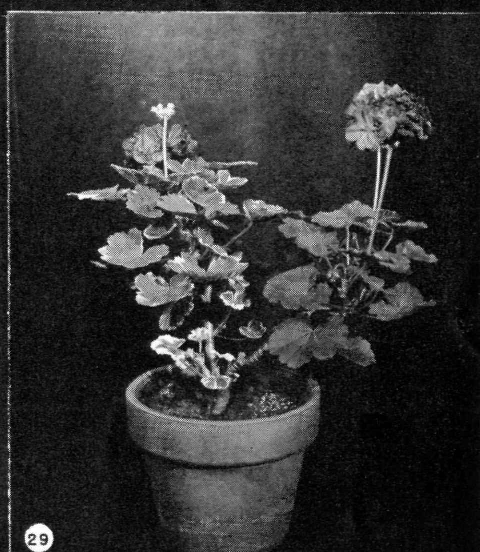
As stated previously all cells of the vegetative parts of a seed plant ordinarily are diploid, established by the fusion of the two monoploid gametes. The diploid, number is maintained by the mitotic cell divisions. In this kind of division, the chromosomes set is duplicated in every division. Occasionally an accident happens which prevents the formation of a new cell plate and the duplicated chromosomes remain together in one cell. The diploid number is doubled by this method and the cell is a tetraploid. If this accident should occur as the zygote divides then every cell of the embryo, seedling and mature vegetative individual will be tetraploid. If it occurs in one cell of a two-celled embryo then the shoot may be tetraploid and the root diploid, or vice versa. If it occurs in a somewhat older embryo, then only that portion of the shoot derived from the original tetraploid cell will have the $4n$ number of chromosomes with other parts remaining diploid. This tetraploid state may occur spontaneously or it may be induced by treatment with colchicine and a few other reagents. Tetraploid plants, in general, may have thicker leaves, larger stems and increased size of the flowers, fruits and seeds. Such plants are usually slower in growth, and consequently are later in flowering and fruiting. The Burpee Seed Company has been advertising tetrasnapdragons and marigolds for several years.

Somewhere in Western Mexico, the tetraploid condition developed in the annual teosinte mentioned previously. The tetraploid plant has 40 chromosomes and is a perennial. The annual teosinte has 20 chromosomes. The tetraploid form has been described as a new species.

Some nurseries list as available a hybrid Horse Chestnut (*Aesculus carnea*). It is a tetraploid, having 80 chromosomes and will "come true" from seed. It is known to have resulted from a cross between the Horse Chestnut (*Aesculus hippocastanum*) with 40 chromosomes and the Red Buckeye (*Aesculus pavia*),







26. Ulrey's variegated African Violet.
27. A variegated specimen of Orchid Wonder variety of African Violet.
28. Mme. Selleroi Geranium.
29. Silver Leaf, S. A. Nutt Geranium.

also having 40 chromosomes. With the exception of one case the hybrids were sterile. In the one instance doubling of the chromosomes must have occurred, resulting in a complete set of Horse Chestnut chromosomes and a complete set from the Red Buckeye in the hybrid zygote. The chromosomes at meiosis could pair and separate in the usual way, and the usual segregation in a hybrid was prevented. This illustrates how a new species may be synthesized through hybridization and the doubling of chromosomes.

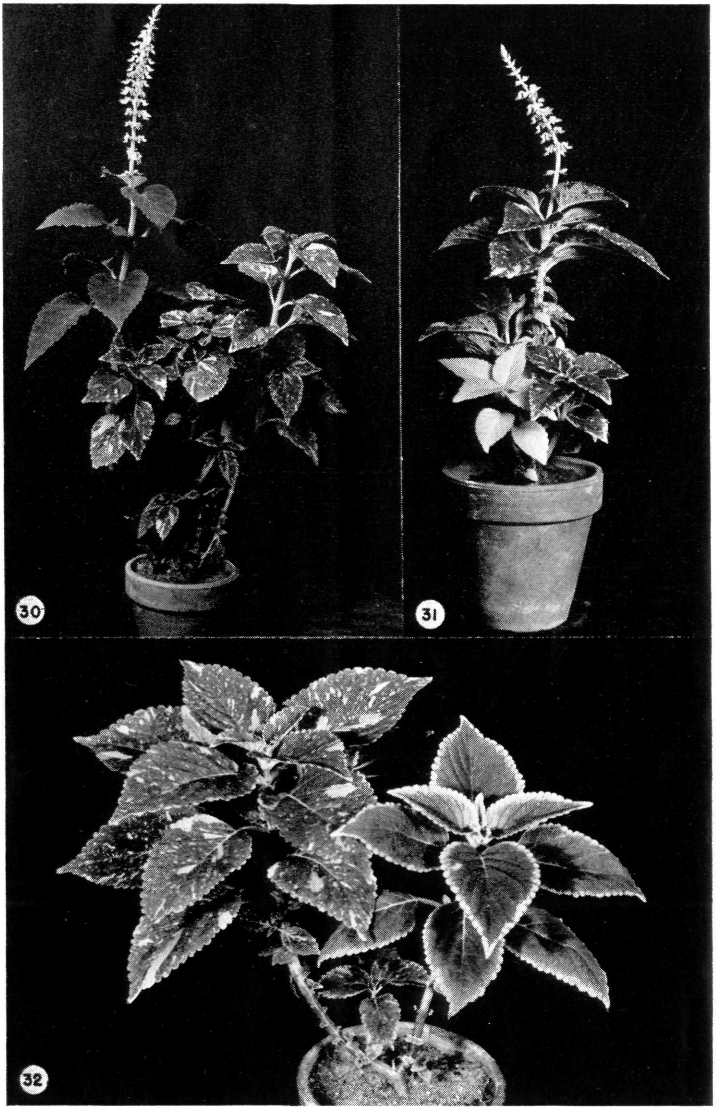
The bread wheat, as mentioned earlier is thought to have arisen in the region of ancient Babylonia. Bread Wheat has 42 chromosomes. Emmer (*Triticum dicoccum*) with 28 chromosomes, another wheat somewhat useful as livestock feed, crossed with a noxious weed, Goat Grass (*Aegilops squarrosa*) with 14 chromosomes, and became the parents of the world's most valuable food plant! This must have occurred by the doubling of the chromosomes in the zygote (fertilized egg) or by the fusion of two unreduced gametes, giving the same result. This kind of heritable variation is by no means uncommon, as one might be led to believe from the above illustrations. It is probable that similar changes were involved in the origin of such domesticated plants as the Potato, Sugarcane, Brome Grass, Cotton, Tobacco, Oats, Apples, Pears and Strawberries.

MUTATIONS

In addition, new, unpredictable, heritable changes in plants may occur, known as gene mutations. Genes are invisible units of the chromosomes, each with a potentiality which may become expressed as an observable characteristic of a plant or animal. Ordinarily genes are stable, remaining unchanged through many generations bridging millions of years. At the other extreme, there are genes which are unstable and mutate frequently in the same way. An illustration of this is found in a corn variety known as "Variegated Pericarp" or "Calico". This maize variety is characterized by the pericarp of the grain being finely variegated with red stripes orientated lengthwise of the grain. Each red stripe or sector is the result of a mutation as shown by Emerson 1914, 1917, and studied recently by Anderson and Brink 1952. Occasionally grains were found which had an entirely red pericarp. The gene controlling the red color is stable, since when red grains are planted every grain on the ear borne by the plant from the red grain, are red. For about 10 years, the writer has had a strain of Calico maize in culture for another purpose. During that time four ears have been found, each with a block of grains with colorless pericarp (fig. 23). When these colorless-pericarp grains are planted, ears are borne every grain of which is colorless. This may represent a mutation in the unstable gene to one that is stable as far as colorless pericarp is concerned.

Mutations may occur in the formation of gametes, or in any living vegetative or somatic cell. In vertebrate animals and in some plants, mutant cells in somatic or vegetative tissues are lost with the death of the individual or at least death of the organ in which it occurred. This has given rise to the too common notion that mutations only occur in the formation of gametes. No techniques are known at present by which pieces of somatic tissues or organs of vertebrate animals or the vegetative organs of some plants can be used in the propagation of such organisms. However, most seed plants may be propagated vegetatively from leaves, stems, or roots. A mutant cell in any one of these organs then has chance at survival, providing the organ is placed in proper conditions which will lead to vegetative multiplication.

If a mutation occurs in a gamete or in the fertilized egg every cell of the embryo is identical to the zygote, as far as chromosomes and genes are concerned. This continues to be true for all cells of the seedling as well as the mature plant. This was mentioned earlier when dealing with growth and development of maize zygotes. Ordinarily when this happens, the mutant individual may be found among many



FIGS. 30–32. Mutations from a splotched leaf type of variegated *Coleus*.

individuals of the parent type which do not exhibit the change. An example of such a mutant is illustrated by (fig. 26) Ulrey's variegated *Saintpaulia* (African Violet). This variegation is due to a chlorophyll deficiency in the young leaves, and is gradually lost as the leaves become older, with old leaves often being entirely green. More variegated plants may grow vegetatively from leaf-cuttings.

Previously it was mentioned that mutations may also occur in any vegetative or somatic cell. This may be illustrated by the African Violet variety sold as "Orchid Wonder". The leaves of this variety are ordinarily dark green in color. The plant illustrated by figure 27, grew vegetatively from the petiole of a detached leaf of the Orchid Wonder variety when placed in moist sand. The chlorophyll deficient tissue resulted from a cell which mutated in the stem primordium which developed near the cut end of the petiole of the detached leaf. As the stem primordium grew, the mutant cell increased in numbers and the chlorophyll deficient tissue became distributed in many of the leaves seen in the illustration. Each variegated leaf then is made up of two genetically different tissues instead of one, as is usual. When variegated leaves of this African Violet, are used as propagules, the young plants are usually green as typical of the original parent, or they are so chlorophyll-deficient that adequate sugar is not made and they soon die of starvation. The variegated state can be propagated from stem cuttings but this is difficult, and not practical since the internodes of the stem are very short and ordinarily there is only one terminal, vegetative bud. The lateral or axillary buds ordinarily are inflorescence buds and their growth is determinate. Similar mutants have been observed in plants derived from leaf cuttings in varieties sold under the name of "Mentor Boy", "Red Head Girl" and "White Lady". The same kind of mutation has probably occurred in many varieties of *Saintpaulia*.

In most variegated plants, the stem internodes are much longer than in *Saintpaulia* and the axillary buds are more likely to be vegetative rather than reproductive. Examples of this will be recognized in the common varieties of Geranium (*Pelargonium*) and *Coleus*. In such examples numerous *stem* cuttings may be made from a single plant. If these stem cuttings are chimaeras, then the chimaeral or variegated condition may be propagated. Mutant tissues in a chimaera may be distributed in a plant organ in one of three ways: (1) Periclinal, (2) Sectorial, and (3) Mericlinal. The periclinal chimaeras are the most stable of the three types. This one is characterized by the mutant tissue forming a solid sheath about the whole organ. The red skin of a Red Triumph potato tuber (fig. 38 a-b) is an example. The sectorial type (fig. 39, 40) is the least stable as far as the chimaeral condition is concerned. The mericlinal type is characterized by an uneven distribution of the mutant tissue in the organ, forming streaks, splotches or mosiac patterns. The mericlinal type is less stable than the periclinal, but more permanent than the sectorial form. Most variegated ornamental plants fall in this class.

The variegated Geranium (*Pelargonium*) listed as "Silver Leaf, S. A. Nutt" (fig. 29) is a fairly stable chimaera exhibiting albino tissue about the border of the leaf-blade. When branched plants are cut back and lateral buds are forced to develop, occasionally a stem is found which bears green leaves with no variegation (fig. 29). Less frequently an albino branch may develop laterally from a larger stem which bore typically variegated leaves. Cuttings from the green branch will multiply vegetatively and continue to be entirely green. Cuttings from the albino branch will not survive because of the lack of sugar.

Another variegated Geranium (*Pelargonium*) variety "Mme. Salleroi", has a chlorophyll-deficient (yellow-green) area radiating from the petoiole-end into the leaf blade (fig. 28). This variegated condition ordinarily is quite stable. However, figure 28 illustrates a plant which has a completely green branch and one which is chlorophyll deficient, in addition to branches which have typically variegated leaves. Cuttings from the green branch will reproduce vegetatively, continuing to be green, and presumably like the parent of this variegated variety.

Cuttings from the mutant yellow-green branch will root and continue to grow with all new leaves and branches having the chlorophyll-deficient color. It is less vigorous and more care is necessary in keeping conditions right for growth.

The above two Geraniums (Silver-Leaf, S. A. Nutt and Mme. Salleroi) illustrate how mutations occurring in vegetative parts may result in chimaeras. The mutation may have occurred but once for each variety, many years ago and the

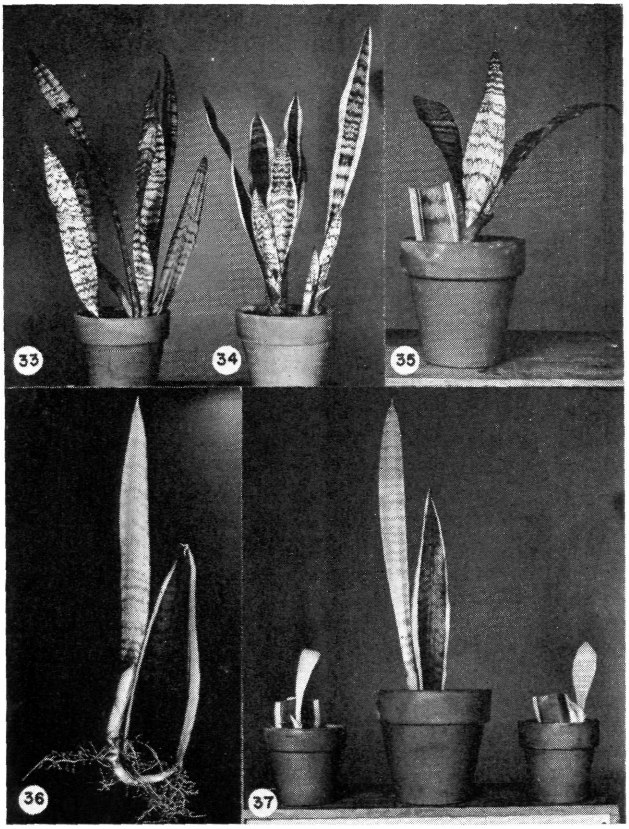


FIG. 33. *Sansevieria trifasciata.*
FIG. 34. *Sansevieria trifasciata,* var. *Laurentii.*
FIG. 35. *S. trifasciata* shoot developing from a leaf-cutting of var. *Laurentii.*
FIGS. 36–37. Yellow shoots originating from yellow tissue of a leaf-cutting of var. *Laurentii.*

mutant chimaeral or variegated state has been maintained by vegetative multiplication. Most variegated plant varieties may be used to demonstrate a mutant individual. The exceptions are found in some varieties which have genetic patterns characteristic of some *Coleus* varieties, and albino spots, blotches or streaks due to viruses as in *Abutilon pictum* (Flowering Maple). The Geranium specimens illustrated in figures 28 and 29, demonstrate vegetative or somatic segregation of the mutant tissue from the chimaera as well as segregation of the original type—the green branches. Obviously meiosis is not involved in this segregation, but is due to fortuitous anatomical deviations. For centuries man has been taking advantage of these vegetative or somatic segregates ("sports" of the older horticultural literature) without much of an understanding or appreciation of how they came about. It has been of great importance in obtaining new and useful plant varieties not only among ornamentals, but most modern varieties of apples, pears, grapefruits, oranges, peaches, grapes and many others.

An unnamed variegated *Coleus* variety, with leaves characterized by a dark red background with flecks of yellow distributed without any particular order or constant pattern, was maintained in culture for several years. From one plant a branch developed which bore completely red leaves (fig. 30). Cuttings from this branch have continued to be dark red in color without any indication of yellow flecks. Figure 31 is a photograph of a plant of the same variety exhibiting a yellow-leafed branch. The yellow branch propagated vegetatively, and continued to be entirely yellow, with the characteristics of the commercial Golden Bedder variety. A third mutation was observed from the same unnamed variety and is illustrated by figure 32. The mutant branch bore leaves which were red with a yellow border around the edge of the leaf-blade. Several similar mutations resulting in chimaeras, have been found in *Coleus*.

The vegetative or somatic segregation of mutant tissues from a chimaera often is not as readily accomplished as in Geranium and *Coleus*. Special methods may have to be employed as described below for potato and *Sansevieria*. Some years ago it was noted that in the common potato variety, "Red Triumph" tubers could be found which had irregular white areas surrounded by the usual red skin, as illustrated by A and B of figure 38. This seemed to indicate that at least these particular tubers were chimaeras, usually of the periclinal type, but by some anatomical deviation, the mericlinal form might develop, as shown for those with white areas in the skin. No bud was found isolated in the white areas which was free of the red pigment. Since the potato is propagated vegetatively from tuber-cuttings having at least one "eye" or bud, it seemed probable that the red-skin character was transmitted to the new vegetative generation by the outermost layers of embryonic cells in the stem tip of the bud. To shorten a long story, the stem tips on numerous cuttings were "peeled" and planted. Some cuttings survived the peeling treatment and developed as usual-appearing potato plants, except for being slower in sprouting. In late summer when the tubers were harvested from the treated plants, most plants bore tubers all of which were variegated, and were interpreted as being mericlinal chimaeras. These probably resulted from incomplete removal of all red tissue from the embryonic stem tip at the time of peeling. A few plants bore tubers all of which were *white* (fig. 38 C) including the "eyes" or stem tips. During the following summer, cuttings from the white tubers were planted, all of which developed plants bearing "White Triumph" potatoes. Two other varieties, "Blue Victor" and "Blue Meshanoc" have been treated in a similar way, resulting in a "White Victor" and a "White Meshanoc" potato.

Bowstring-Hemp or snakeplant (*Sansevieria trifasciata*) (fig. 33) has been in cultivation as an ornamental for more than a century and as a fiber plant in Africa for a much longer time. About fifty years ago a variegated form, characterized by a golden-yellow border around the leaf-edge, was found in cultivation by a native tribe in the Belgan Congo. It was named *Sansevieria trifasciata* var. *Laurentii*, and is usually listed on the floral market as *S. Laurentii* (fig. 34). This variety is more popular today as a decorative plant than is the species. The species (fig. 33) could propagate vegetatively from leaf-cuttings as well as from rhizome pieces having a stem tip. Soon after the variegated variety (*Laurentii*) was introduced as a house-plant it was learned that the variegated form could be propagated only from rhizome cuttings. When leaves are used as propagules, non-variegated plants will result from them which are like the species as illustrated in figure 35. This led to the inference that *Laurentii* is a chimaera with two genetically different tissues. That is the golden-yellow tissue, forming a border to the leaf, is genetically different from the green tissue. To test this inference, leaf cuttings were made as illustrated in figure 36. This was done because roots develop from the cut end when in contact with moist sand. However, ordinarily roots develop only from the green tissue of the leaf cutting and not from the yellow tissue. New shoots or stems initiate at the base of a root about where the root originates from the leaf tissue. A block of all-green tissue was removed from the area of the leaf cutting which was to be set in moist sand, with only strips of yellow tissue in contact with the substrate. Roots, after some time, developed from the yellow tissue and eventually golden yellow shoots as illustrated in figures 36 and 37. At first the shoots are slightly green, indicating the presence of some chloroplasts, but these soon disintegrate and the tissues become golden-yellow

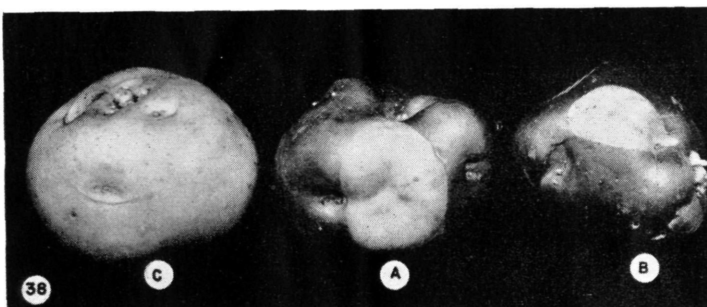


FIGURE 38. A and B, Chimaeral tubers of the Red Triumph Potato. C, White tuber which resulted from peeling a bud from Red tuber used as a propagule.

FIGURE 39. A sectorial chimaera of grapefruit.

in color. If the rhizome connection between the yellow shoot and the leaf-cutting is broken, the shoot dies of starvation within about two weeks. This is presented as evidence that the yellow tissue is genetically different from the green. The yellow tissue is mutant tissue which has existed in a chimaeral relationshup with green *Sansevieria* tissue, perhaps much longer than the fifty years since the French botanist Laurent, discovered it in cultivation by natives of the Belgan Congo. It is only by accident, or when special technique as described above is applied, that segregation of the pure yellow mutant tissue results in chlorophyll deficient plants.

Mutations resulting in sectorial chimaeras may occur in leaves, stems, roots, inflorescences, flowers and fruits. The grapefruit illustrated by figure 39 had a relatively large sector of the fruit coat or pericarp which was dark brown in color in contrast to the light yellow color of the remainder of this particular fruit. No differences were observed in the carpels containing the pulp oposite the brown sector of the pericarp and those opposite the yellow part of the fruit coat. The inference from this and other evidence was that only the sector of the pericarp was affected by this mutation and that the carpels and seeds opposite the brown sector were not changed. Similar sectoring is fairly frequent in oranges, lemons and grapefruit.

Sectorial chimaeras in fruits are not always superficial, *i.e.*, limited to the pericarp. Several years ago a tomato fruit of the Baltimore variety (fig. 40) was found in a field, which had a sharply outlined yellow sector with the adjoining parts of a deep red color. Eventually a cross-section of the fruit was made in order to examine the extent of the yellow mutant tissue of the sector. It was readily evident that the yellow tissue extended to the center of the fruit and included two seed cavities.

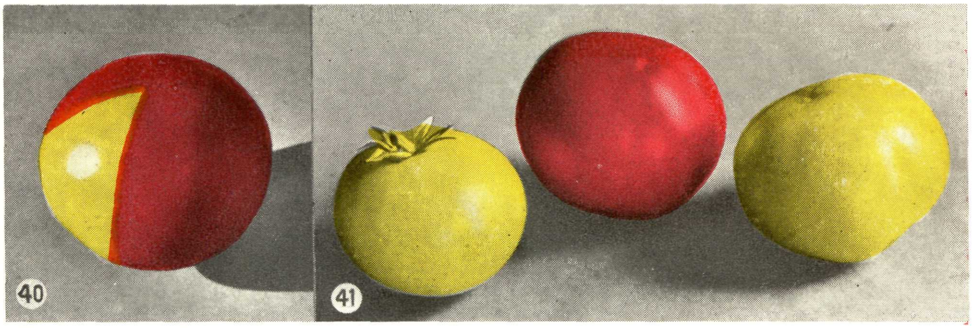


FIGURE 40. A sectorial chimaera of a tomato fruit.

FIGURE 41. Plants from seed of the yellow sector (fig. 40) bore yellow tomato fruits, while those from the red portion of the chimaera continued to bear red fruits—second fruit from left.

Seeds from the yellow sector were saved as well as those from the red portion of the fruit. Three plants from seeds of the yellow sector, matured and bore yellow fruits (fig. 41). Descendants from these three plants have been carried through ten generations with the matured fruits of each generation continuing to be yellow.

Seeds were also saved from the red portion of the chimaeral fruit (fig. 40) and planted. All the progeny bore red fruits. Two lines were selected from these red-fruited plants as sources of seed. Descendants of these two plants have been planted for ten generations with no segregation of yellow fruits having been observed and no more fruits have been found with yellow sectors.

Yellow fruiting plants were cross-pollinated with red fruiting plants. The hybrid plants (F_1 Generation) all bore red fruits as might be anticipated from results upon crossing other varieties of red and yellow tomatoes, and illustrates the dominance of the red color factor over yellow color. Seeds were obtained from self pollinated hybrids and planted. Out of a group of 59 plants, 45 bore red fruits and 14 were yellow fruited, working out as a simple Mendelian 3:1 ratio.

Although no other sectorial chimaera has been reported for fruits, from which the mutant character is transmitted by seed, it probably does occur and usually escapes unnoticed. This suggests another plant organ and place in the life cycle worthy of close observations, where mutants may be discovered.

This story of the domestication of plants is a story of how man has and is now making use of the products of evolution which are desirable to him. The world is represented in our gardens, orchards, and fields by many domesticated plants, necessary in our daily activities and well being. Achievements have been considerable in the past, and there still remains a great reservoir of unexplored plant potentialities.

REFERENCES

Ames, O. (1939). Economic annuals and human cultures. Botanical Museum of Harvard University, Cambridge, Mass.

Anderson, E. (1952). Plants, Man and Life. Little, Brown and Company, Boston.

Anderson, R. E., and **R. A. Brink.** (1952). Kernel pattern in variegated pericarp maize and the frequency of self-colored offspring. Amer. Jour. Bot., 39: 637–644.

Bird, J. B. 1948). America's oldest farmers. Nat. Hist., 57: 296–303, 334–335.

Bryan, K. (1941). Geologic antiquity of man in America. Sci., 93: 505–514.

Camp, W. H. (1947). The world in your garden. National Geog. Mag., 92: 1–66.

Carter, G. F. (1945). Plant geography and culture history in the American Southwest. The Viking Fund, Inc., New York.

Emerson, R. A. (1914). The inheritance of a recurring somatic variation in variegated maize. Amer. Nat., 48: 87–115.

———. (1917). Genetical studies of variegated pericarp in maize. Genetics, 2: 1–35.

Hodge, W. H. (1949). The goliath of seeds. Nat. Hist., 58: 34–35.

Libby, W. F. (1951). Radiocarbon dates II. Sci., 114: 291–296.

Mangelsdorf, P., and **R. G. Reeves.** (1939). The origin of Indian corn and its relatives. Texas Agr. Exp. Sta. Bull. No. 574.

Merrill, E. D. (1937). Domesticated plants in relation to the diffusion of culture: Early man. Edited by G. G. McCurdy, Philadelphia.

———. (1933). Crops and civilization. Nat. Hist., 33: 235–250.

Weatherwax, P. (1950). The history of corn. Sci. Monthly, 71: 50–60.